

WHY DO "FAMILY SPIDERS", *STEGODYPHUS* (ERESIDAE), LIVE IN COLONIES?

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ABSTRACT

In the social eresid spider *Stegodyphus mimosarum*, most individuals under natural conditions live in colonies containing up to several hundred individuals. Female size at maturity is reduced in large colonies as is the number of eggs produced per female. This reduction of female fecundity seems to result from increasing competition over food as the number of females in a colony increases, and is interpreted in terms of a "constraint" model for group living proposed by Emlen (1984).

INTRODUCTION

Cooperative societies have arisen independently in several taxa of spiders. Since social spiders cooperating in predation regularly capture larger prey than solitary spiders of a similar size, it is generally assumed that the greater ease with which prey can be caught and killed by a group accounts for communal hunting and has promoted the evolution of social life in spiders (Brach 1977; Buskirk 1981; Nentwig 1985). But studies performed in the field and in our laboratory on *Stegodyphus mimosarum* Pavesi, one of the most social spider species, have shown that (1) the increase in prey availability does not keep pace with increasing spider numbers and feeding becomes less efficient as group size increases; (2) colony members compete over food, the more so the larger the colony; (3) spiders from larger colonies are smaller than those from smaller colonies; and (4) most colonies are larger than are optimal for individual spider's growth (Ward and Enders 1985; Ward 1986). On the other hand, spider reproductive output is a function of the intake of prey biomass, and fecundity correlates with spider size (Craig 1987). To answer the obvious question, how group-living affects female fecundity in *S. mimosarum*, we determined the numbers of egg-cocoons, and the numbers of eggs in them, for colonies of different sizes.

MATERIAL AND METHODS

Stegodyphus mimosarum, locally known as "family spider", inhabits African dry thornbush country, living in colonies in compact, sponge-like silk nests with tubular passages inside which the spiders tend to remain during the day. One or more trap sheet-webs carrying very adhesive cribellar silk are attached to the nest and stretch to nearby twigs, catching a variety of insects. The species reproduces

between November and March and has an annual life cycle (Seibt and Wickler 1988).

For an analysis of the nest contents and of the composition of colonies we collected 56 *S. mimosarum* nests during Nov./Dec. in the years 1982, 1984 and 1985 from eastern Transvaal and north-eastern Natal (South Africa). The nests were carefully dissected and all inhabitants (a total of 2298 females and 249 males) counted and measured. Size of the live individuals is given as total body length (prosoma plus opisthosoma), measured to ± 0.1 mm with a vernier calliper. Female sexual maturity was checked from the external appearance of the epigynal opening (following O. and M. Kraus 1988). We refer to the number of female spiders living in a given nest as "colony size". Males are omitted as they occurred in very low numbers and do not spin trap webs. Statistical tests used were Spearman's coefficient of rank correlation r_s , Pearson's correlation coefficient r , Mann-Whitney U -test, Student's t -test, all following Sokal and Rohlf (1981).

RESULTS

Female size at maturity.—Colony size varied between 1 and 372. Even with the unaided eye it was apparent that mature females from large colonies were smaller than those from small colonies. We measured 29 mature females from a colony containing 42 females and they were 8.4 ± 0.6 mm (mean \pm SD) long. Also measured were 105 females from the largest colony (372 females) which had an average length of 6.5 ± 0.7 mm. The difference is highly significant (t -test, $p < 0.0001$).

Numbers of eggs and of cocoons.—Eggs of *S. mimosarum* are about 0.5 mm in diameter. They are deposited in flat, circular cocoons of about 5 mm diameter.

Egg numbers for 32 cocoons, taken from 7 colonies, ranged from 15 to 48. The average egg number per cocoon was $26.3 (\pm 8.6)$. No counts are available for colonies containing more than 30 females. For smaller colonies, the number of eggs per cocoon decreases with increasing colony size (Fig. 1a). Taking all 32 counts as independent data, the decrease is significant ($r_s = -0.448$, $p = 0.01$); the average egg number per cocoon for each colony still gives a negative, though a non-significant $r_s = -0.5455$ ($n = 7$).

In 29 nests we found between 1 and 20 egg cocoons per nest. There was no significant correlation between the number of cocoons and the number of either all females ($r_s = 0.316$, $p = 0.095$), or only mature females ($r_s = 0.419$, $p = 0.074$), in a colony.

Thus, neither the number of eggs per cocoon nor the number of egg cocoons present increases significantly with the number of females (mature, or all) in a colony. Even when we neglect a possible tendency towards reduced egg number per cocoon in larger colonies, the per capita reproductive output, as indicated by the ratio of cocoons per female over number of females in the colony (Fig. 1b) suggests an exponential decrease. Indeed a log-log-transformation gives a significant negative linear regression (Pearson $r = -0.772$; $p < 0.0001$) which fits the data significantly better than a linear regression with the untransformed data ($r = -0.434$; $p = 0.019$): the difference between the correlation coefficients is significant ($p < 0.05$; $x = 4.084$; $df = 1$. Sachs 1969). We conclude, therefore, that an individual's expected reproductive output shows a constant allometric decline with increasing colony size.

This fact refers to the reproductive output measured at a given time. In theory, larger colonies, or at least a considerable fraction of their female population, might reproduce later, and the number of cocoons present at the time of collection might be a less reliable measure of the total number of cocoons produced for larger than for smaller colonies. We therefore compared our chances of finding cocoons in small and large colonies. We divided the total of 56 colonies analyzed into two sets according to whether they contained cocoons (29 colonies) or not (27 colonies). Sizes of colonies with cocoons (median 21 females, range 1-372, quartiles 7.5 and 49.5) did not differ significantly from sizes of colonies without cocoons (median 12, range 1-351, quartiles 4.0 and 25.0); *U*-test, $p = 0.09$. But colonies with cocoons tended to be larger rather than smaller compared to colonies without cocoons.

DISCUSSION

All colonies analyzed were long-established ones, as could be seen from the perfect nest construction. Immigration of individuals into established colonies has never been reported and is highly unlikely in view of the colony distribution in the field. A rich local food supply seems to relate to a higher number of colonies in a given patch rather than to an increase in colony size (Seibt and Wickler 1988). Colony growth seems to result from reproduction over successive generations only. But even if an increase in colony size was favored by prey availability, individual spider size obviously does not keep pace, as shown by the size of the mature females in the colonies. Although females may emigrate to start new colonies, the largest females tend to stay in the nests while intermediate-sized individuals are more likely to leave, as Ward (1986) found with experimental *S. mimosarum* colonies.

Smaller body size of mature females in larger colonies is in line with Ward's (1986) finding that as nest size increases, the mean weight of the spiders (not checked for maturity) decreases. This is best understood as a consequence from competition which increases with group size.

Competition over food is easily observed in *Stegodyphus*. The seemingly cooperative subduing of prey, where several spiders grab one insect appendage each and pull backwards, making it impossible for the insect to struggle free, results from each spider's tendency to secure the whole prey for itself; small prey items are in fact carried home by a single spider, as are parts of a larger item should it break into pieces. In the laboratory, spiders in smaller groups were more cooperative and less competitive than those in larger groups (Ward 1986), and feeding became less effective as group size increased (Ward and Enders 1985). This suggests that indeed there is a smaller amount of food available to each spider as colony size increases.

In a recent synopsis of available data, Craig (1987) states that (a) within-species variation in spider size at sexual maturity seems to be a function of local variation in food availability, and (b) spider reproductive output is a function of the intake of prey biomass. As shown here, mature *S. mimosarum* females taken from a large and a small colony differ in average size by more than 2 mm. It seems unlikely that a spider can increase its total length by 1/4 or 1/3 after having reached sexual maturity. Thus we assume that mature females in a large

colony could never attain the size of females in a small one. And as the cocoon counts show, smaller body size of females in larger colonies seems to be linked to lower fecundity as a result from sociality.

Admittedly, the exact amount of reduction in reproductive output caused by social life cannot be assessed at present since it partly depends on the consequences of kin association which is only superficially known for *Stegodyphus*. Also, lowered total offspring number could be compensated by lowered offspring mortality, i.e., reproductive output times the probability that offspring become adults may be the relevant measure, as shown by Smith (1982) for the facultatively communal spider *Philoponella oweni* (Chamberlin) (Uloboridae). Riechert (1985) could rule out the necessity to subdue prey jointly as an explanation for living socially in the spider *Agelena consociata* Denis (Agelenidae); she also found that foraging success and egg production decrease with increasing group size in this species. Originally, Kullmann (1968) suggested that the construction of a safe retreat is a first step toward sociality in spiders; he listed some permanent social species, e.g., *Philoponella republicana* (Simon), which only build communal retreats but catch prey individually.

There are good reasons to assume that *Stegodyphus* offspring benefits from a considerable degree of safety in a large existing nest. Social *Stegodyphus* spiders, by their combined spinning activities, construct a very dense and compact nest. Young spiders hatched in a colony nest usually stay there. Nests are occupied and enlarged by consecutive generations of spiders and may finally attain the size of more than a man's head, acting as protective shields against predators, solar radiation, and presumably also against excessive water loss. Physical protection in a carton-like nest against wind and fire seems to be an important factor facilitating social behavior also in *Diaea* sp. (Thomisidae) (York Main 1986). Individuals emigrating from a *Stegodyphus* colony would seem to be in great danger from predators, as shown for the comparable social spiders *Anelosimus eximus* (Vollrath 1982) and *Agelena consociata* (Riechert et al. 1986). High costs or risks associated with departure seem to operate as constraints, tipping the cost-benefit balance against the choice of personal reproduction in many social groups of cooperatively breeding birds and mammals (Emlen 1984). Available data suggest that this also applies to social *Stegodyphus* and possibly to other social spiders, regardless of whether their sociality evolved via individual, kin or group selection, the latter being proposed by Lubin (1984/85) and Aviles (1986).

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